

AMPHIBIA: ANURA: LEPTODACTYLIDAE

Leptodactylus fragilis

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Leptodactylus fragilis.

***Leptodactylus fragilis* (Brocchi)**
White-lipped Thin-toed Frog

Cystignathus gracilis: Cope 1870:162.

Cystignathus caliginosus: Brocchi 1877:180.

Cystignathus fragilis Brocchi 1877:182. Type-locality, "Cet animal a été envoyé de Tehuantepec (Mexique)." Holotype, Muséum National d'Histoire Naturelle, Paris (MNHN) 6316, female, collected by M. Sumichrast (examined by WRH).

Cystignathus labialis: Cope 1879:265.

Leptodactylus albilabris: Boulenger 1881:30.

Leptodactylus caliginosus: Brocchi 1882:17.

Leptodactylus fragilis: Brocchi 1882:19. First usage associating *fragilis* with the genus *Leptodactylus*.

Leptodactylus gracilis: Cope 1887:17.

Leptodactylus labialis: Ives 1892:461.

Leptodactylus melanotus: Dunn and Emlen 1932:22 (part).

Leptodactylus albilebris: Pratt 1935:164. *Lapsus*.

Leptodactylus mystaceus labialis: Shreve 1957:246.

Leptodactylus labialus: Wilczynski, Rand, and Ryan 2001 [2002]:149. *Lapsus*.

Leptodactylus cf labialis-fragilis: Flores-Villela 1993a: 260.

• **CONTENT.** The species is monotypic.

• **DEFINITION.** Adult *Leptodactylus fragilis* are small. The head is longer than wide, and the hind limbs are moderately long (Table 1; Heyer and Thompson 2000 provided definitions of adult size and leg length categories for *Leptodactylus*). Male vocal

Table 1. Summary measurement data for *Leptodactylus fragilis* (means are in parentheses).

Measurement	Males	Females
SVL (mm)	27-43 (34.8)	30-44 (36.4)
HL/SVL (%)	35-42 (38)	34-42 (37)
HW/SVL (%)	29-38 (34)	29-37 (33)
Thigh length/SVL (%)	32-46 (39)	32-44 (39)
Shank length/SVL (%)	39-51 (45)	37-53 (46)
Foot length/SVL (%)	41-57 (49)	40-56 (49)

sacs are laterally expanded and range from lightly gray speckled to darkly pigmented. Male snout is spatulate; female snout is rounded. Male forearms



Figure 1. *Leptodactylus fragilis*, USNM 563465, Rus Rus, Gracias a Dios, Honduras. Photograph courtesy of James R. McCranie.



Figure 2. *Leptodactylus fragilis*, ASU 17034, Starr County, Texas. Photograph courtesy of Wayne Van Devender.

are not hypertrophied and males lack asperities on the thumbs and chest. The dorsum is spotted or blotched with dark markings, which are often chevron-shaped and sometimes confluent. The supratympanic fold is dark brown. A pair of dorsolateral folds is usually poorly developed, extending from the posterior portion of the eye, passing just lateral to the sacral bones and ending in the upper groin region at the leg; the folds are often highlighted by dark and/or light stripes. A pair of lateral folds extends from the posterior dorsal portion of the tympanic fold to the mid-groin level at the leg juncture; the folds are often interrupted and/or poorly developed and are usually of lighter color than the adjacent flanks. The toe tips are rounded, either of equal diameter or slightly greater than the toe portion immediately behind the tip. The toes either lack lateral ridges and basal webbing or have very weakly developed lateral ridges (most developed proximally) and a trace of basal webbing between some or all toes I-II-III-IV. The dorsal surface of the shank is usually covered with many white tubercles, or sometimes the white tubercles are few and scattered. The posterior surface of the tarsus either has many white tubercles (89%), or is smooth (11%). The sole of the foot always has many white tubercles. A light lip stripe extending from under the nostrils, passing under the eye and tympanum and continuing through the commissural gland is usually poorly developed (97%) or rarely distinct (3%). An

interrupted mid-dorsal dark pin-stripe is occasionally present. The belly is often cream colored (lacking melanophores), it may have a scattering of melanophores to scattered diffuse dark blotches anteriorly and on the sides, or there may be scattered melanophores over the entire belly. The posterior surface of the thigh usually has a very distinct light longitudinal stripe on the lower half (66%), often moderately distinct (33%), or rarely absent (1%).

Larvae are exotrophic, lentic, benthic guild members (McDiarmid and Altig 1999, guild IIA1). Larval morphological characteristics of *L. fragilis* were included in the comparisons with other larvae of the *L. fuscus* group by Langone and de Sá (2005). The oral disk is anteroventrally positioned, entire (not emarginated), and has a broad anterior gap lacking marginal papillae. Submarginal papillae, if present, are not clearly distinguishable from the marginal papillae. The tooth row formula is 2(2)/3(1) (see **Remarks**). Tooth row A-2 is broadly interrupted, while row P-1 is narrowly interrupted. Row P-3 is noticeably shorter than rows P-1 and P-2. The spiracle is sinistral and the vent tube is median. The dorsal fin originates at the posterior end of the body. Larval total length at Gosner stage 32–34 ranges from 22–32 mm. Body length of stage 32–41 larvae ranges from 8–12 mm. Tail length is 63–67% of total length. Eye diameter is 12–16% of body length. The width of the oral disk is 17–22% of body length. A lateral line system is not evident. The dorsum of the body is uniformly suffused with melanophores. A greater concentration of melanophores is situated posteromedially to the nostrils (best seen from dorsal perspective). The spiracle is either lighter or not much lighter than its surroundings. The mouthparts and the region immediately posterior to the oral disk are patternless or marked with a few scattered melanophores. The rest of the anterior venter is scattered with melanophores. The posterior portion of the venter and anal tube are either patternless or with very few scattered melanophores. The tail (both musculature and fins) has scat-

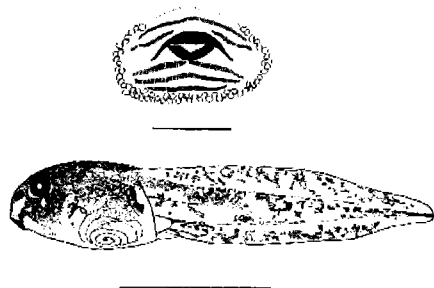


Figure 3. Tadpole of *Leptodactylus fragilis*, figures 7 and 17 in Heyer (1970b), based on specimen from Costa Rica. Upper scale bar = 1 mm, lower scale bar = 10 mm. Tail myotomes not illustrated.

tered groupings of melanophores forming blotched patterns.

The advertisement call consists of a single note (usually) or two notes per call given at rates of 120–

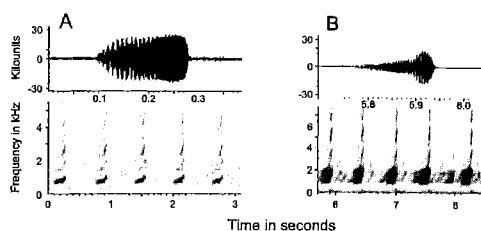


Figure 4. Wave form and audiospectrogram displays of the advertisement call of *Leptodactylus fragilis*. Wave form of first call in the audiospectrograms. A – USA, Texas, Hidalgo County, 2 miles east Madero, air temperature 28° C (Tape Station 29, Texas Memorial Museum recording). B – Venezuela, Estado de Zulia, Santa Barbara, air temperature 24° C (USNM recording 225, cut 2).

150 calls/min (Belize, Texas USA), 1.5–71 (Colombia), 104 (Costa Rica), 79 (Panama), and 86–93 (Venezuela). Call duration varies from 0.16–0.20 s, except the range from a Colombian population is 0.11–0.19 s. The call is amplitude modulated consisting of (a) either a single note of 22–25 pulses, (b) a single note with 9–10 pulses in the first half of the call with pulses becoming indistinct in the second half, or (c) two notes, the first note with 22–30 partial pulses, the second note either unpulsed or with 2–3 partial pulses. The call, a rising harsh whistle, is frequency modulated and either has a short drop in frequency at the very beginning and very end of the call (Panama) or rises throughout (Texas USA, Venezuela). The first part of the call (about 60–75% of total call duration) has a lower rate of frequency increase than the second part which has a rapid rise in frequency. The call begins at about 600–750 Hz (Texas USA), 810–940 Hz (Venezuela), 890–1020 Hz (Panama) or 1000 Hz (Belize, Costa Rica) and ends at about 1000–1200 Hz (Texas USA), 1700 Hz (Costa Rica), 1820–1920 Hz (Venezuela), 1970–2010 Hz (Belize, Panama), or 2200 Hz (Panama). Two patterns of intensity modulation occur in the available recordings. The first pattern except Texas USA) has a steady increase in energy during approximately the first 60% of the call, a rapid increase in energy ending at maximum loudness in about the next 25% of the call, and a rapid drop in loudness in approximately the final 15% of the call. The second pattern (Texas USA recording) has a fast rise of intensity during the first 25–33% of the call followed by steady or slight decrease of intensity during the next 20–30% a weak increase in the next 33%, a slow drop in the next 5–7% and a sharp drop of intensity in the final 5–7% of the call. The dominant frequency is the fundamental frequency and ranges from 740–780 Hz (Texas USA), 1720–1775 Hz (Venezuela), or 1865–1940 Hz (Panama). The call has a well-developed harmonic structure (see **Remarks**).

• **DIAGNOSIS.** The small species of *Leptodactylus* without distinct toe fringes, indistinct dorsolateral folds, a light longitudinal stripe on the lower portion of

the thigh, and obvious white tubercles on the dorsal surface of the shank and sole of the foot are *L. caatingae*, *fragilis*, and *latinasus*. There is considerable morphological overlap among these three species and they cannot be consistently diagnosed from each other based on morphological characters. The advertisement call of *L. fragilis* is longer (0.11–0.20 s) than the call of *L. caatingae* (0.07 s.). The advertisement call of *L. latinasus* is not pulsed (pulsed in *L. fragilis*) and the dominant frequency is higher (3000–3780 Hz) than that of *L. fragilis* (maximum 2200 Hz).

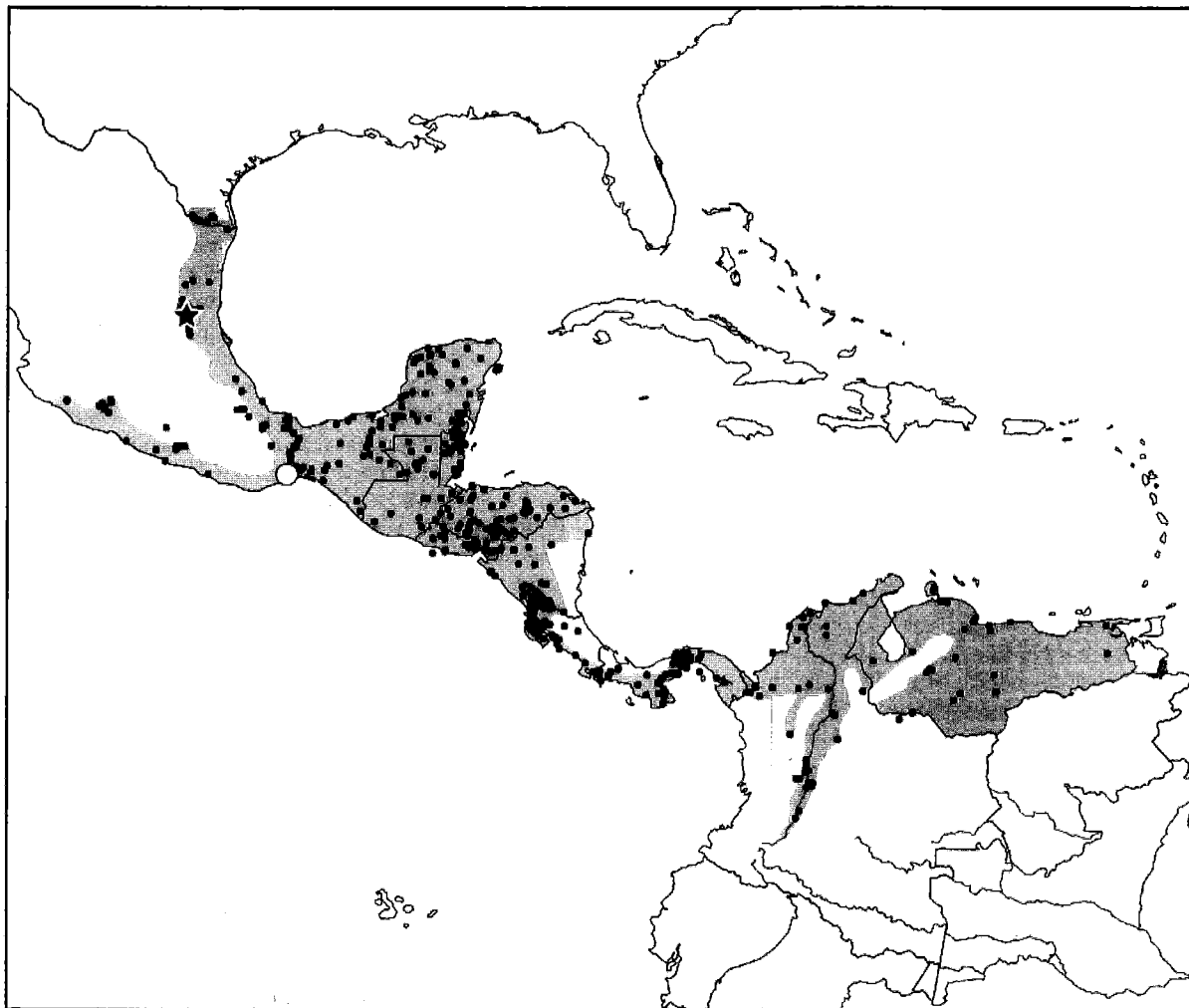
• **DESCRIPTIONS.** Brocchi's (1877) original description of the species included details of morphology and color. Additional descriptions of morphological characters and color may be found in Boulenger (1882), Brocchi (1882, as *L. labialis* and *L. caliginosus*, in part), Campbell (1998, as *L. labialis*), Günther (1900, as *L. fragilis* and *L. albilabris*, in part), Heyer (1970b, 1971, both as *L. labialis*, 1978, as *L. fragilis*), Ives (1892, as *L. labialis*), Kellogg (1932, as *L. albilabris*), Köhler et al. (2005, as *L. fragilis*), Lee (1996, 2000, as *L. labialis*), Maslin (1963b, as *L. labialis*), McCranie et al. (2006, as *L. fragilis*), McCranie and Wilson (2002, as *L. labialis*), Nieden (1923, as *L. fragilis*), Noble (1918, as *L. albilabris*), Rendón R. et al. (1998, as *L. labialis*), Ruthven (1912, as *L. albilabris*), Savage (2002, as *L. labialis*), Taylor (1932, as *L. albilabris*, 1954, as *L. labialis*), and Wright and Wright (1933, a secondary source as *L. albilabris*, in part). Larval characteristics and color are found in Campbell (1998, as *L. labialis*), Heyer (1970b, 1971, both as *L. labialis*, 1978, as *L. fragilis*), Lee (1996, 2000, as *L. labialis*), Maslin (1963a, as *L. labialis*), McCranie and Wilson (2002, as *L. labialis*), Mulaik (1937, as *L. labialis*), and Savage (2002, as *L. labialis*). Eggs of the species were described by Maslin (1963a, as *L. labialis*), while Maslin (1963b, as *L. labialis*) and Mulaik (1937, as *L. labialis*) characterized the foam nest. Descriptions of the advertisement call of *L. fragilis* are included in Fouquette (1960b, as *L. labialis*), Heyer (1971 as *L. labialis*), Lee (1996, as *L. labialis*), and Straughan and Heyer (1976, as *L. labialis*). Bogart (1974, as *L. labialis*) provided a description of the karyotype.

• **ILLUSTRATIONS.** Photographs of *L. fragilis* can be found in Bartlett (1999, as *L. labialis*), Bartlett and Bartlett (1999, as *L. labialis*), Behler and King (1979, as *L. labialis*), Bernal (2002, as *L. fragilis*), Bogart (1974, as *L. labialis*), Campbell (1998, as *L. labialis*), Conant (1991, as *L. labialis*), Cuentas Montalvo et al. (2002, as *L. labialis*), Freiberg (1972, as *L. labialis*), Garrett and Barker (1987, as *L. fragilis*), Heyer (1970b, as *L. labialis*), Höbel (2004b, as *L. labialis*), Ibáñez D. et al. (1999a, as *L. labialis*), Köhler (2001, as *L. labialis*), Köhler et al. (2005, as *L. fragilis*), Lee (1996, 2000, both as *L. labialis*), McCranie et al. (2006, as *L. fragilis*), McCranie and Wilson (2002, as *L. labialis*), Mertens (1952a, as *L. labialis*), Meyer and Foster (1996, as *L. labialis*), Mudde and van Dijk (1984, as *Rana pipiens*), Norman (1998, as *L. fragilis*), Renjifo and Lundberg (1999, as *L. fragilis*), Sa-

vage (2002, as *L. labialis*), Sennft (1935, as *L. labialis*), Taylor (1954, as *L. labialis*), Vences and Schmitt (1992, as *L. labialis*) and Weimer et al. (1993, as *L. fragilis*). Illustrations of adult specimens are included in the publications of Beletsky (1999, as *L. labialis*), Brocchi (1882, as *L. fragilis* and *L. caliginosus*), Conant (1958, 1975, both as *L. labialis*), Conant and Collins (1991, 1998, both as *L. labialis* and White-lipped [Frog]), Galindo-Leal (2003, as *L. labialis*), Gorzula and Señaris (1999, as *L. labialis*), Heyer (1978, as *L. fragilis*), Norman (1998, as *L. fragilis*), Smith (1978, as *L. labialis*), Wainwright (2000, as *L. fragilis*), Wright and Wright (1933, as *L. albilabris* in part, 1942, as *L. labialis* both secondary sources), Wright and Wright (1949, a secondary source as *L. labialis*), and Zim and Smith (1956, as *L. labialis*). Köhler (1999a, as *L. labialis*), Köhler et al. (2005, as *L. fragilis*), Lee (1996, 2000, as *L. labialis*), Powell et al. (1998, as *L. labialis*), Savage (2002, as *L. labialis*), and Villa (1972, as *L. labialis*) provided drawings of adult hands and feet, while Larson and de Sá (1998, as *L. labialis*) and Wever (1985, as *L. labialis*) illustrated larval chondrocranial characteristics and aspects of the ear, respectively. Larvae are illustrated in Conant and Collins (1998, as *L. labialis*), Heyer (1970b, as *L. labialis*), Köhler et al. (2005, as *L. fragilis*), Lee (1996, 2000, as *L. labialis*), Maslin (1963a, as *L. labialis*), Savage (2002, as *L. labialis*), and Villa (1972, as *L. labialis*). Dixon and Heyer (1968, as *L. labialis*), Höbel (2004b, as *L. labialis*), and Klingelhöffer and Scherpner (1956, as *L. labialis*) pictured foam nests of the species. Sonagrams or audiospectrograms or an oscilloscope trace appear in Bernal et al. (2004, as *L. fragilis*), Blair (1963, as *L. labialis*), Fouquette (1960b, as *L. labialis*), Heyer (1971, as *L. labialis*), Ibáñez D. et al. (1999a, as *L. labialis*), Kime et al. (2000, as *L. fragilis*), Lee (1996, as *L. labialis*), and Straughan and Heyer (1976, as *L. labialis*). Finally, Bogart (1974, as *L. labialis*) included a photograph of the karyotype.

• **DISTRIBUTION.** *Leptodactylus fragilis* is a lowland frog occurring from southernmost Texas (Cameron, Hidalgo, and Starr counties) on the Atlantic coast and Colima, Mexico on the Pacific coast, southward throughout Mexico and Middle America to northern Colombia including the Cauca and Magdalena valleys, the Río Arauca and Río Apure drainages in Colombia and northern Venezuela extending as far as the Venezuelan State of Sucre. The species has not been recorded from the mid-point of the Atlantic coastal lowlands of Costa Rica to the canal region in Panama, nor is it known from the islands of Margarita, Trinidad, or Tobago. Harding (1983, as *L. fragilis*) arranged its distribution by countries in the New World. Campbell (1999, as *L. labialis*) delineated its topographic and ecogeographic distribution in Middle America, while Duellman (1999, as *L. labialis*) tabulated its South American natural region distribution as Caribbean lowlands and Llanos. The species was reported as occurring between sea level and 1590 m.

The following references to distribution, localities and elevation (when provided) are listed by country



Map. Distribution of *Leptodactylus fragilis*. The type-locality is indicated by a circle. The purported fossil locality is indicated by a star. Dots mark other localities. A dot may represent more than one site. Published locality data used to generate the map should be considered as secondary sources of information, as we did not confirm identifications for all specimen localities. The locality coordinate data and sources are available on a spread-sheet at [http:// learning.richmond.edu/Leptodactylus](http://learning.richmond.edu/Leptodactylus).

and the letter (M) indicates species mention for a region with no precise locality data provided, while (S) denotes a secondary source: **Belize** (Campbell and Vannini 1989 [as *L. fragilis*], Fugler 1960 [as *L. labialis*], Henderson and Hoevers 1975 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Larson and de Sá 1998 [as *L. labialis*], Neill 1965 [as *L. labialis*], Neill and Allan 1961 [as *L. labialis*], Schmidt 1941 [as *L. labialis*], and Turvey and Cooper 1999 [as *L. labialis*]); **Colombia** (Acosta-Galvis 2000 [as *L. labialis*], Bernal et al. 2000 [as *L. fragilis*], Bogart 1974 [as *L. labialis*], Cuentas Montalvo et al. 2002 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Lynch and Suárez-Mayoraga 2004 [as *L. labialis*], Páez et al. 2002 [as *L. labialis*], Renjifo and Lundberg 1999 [as *L. fragilis*], and Ruiz-Carranza et al. 1996 [as *L. fragilis*]); **Costa Rica** (Albert et al. 2005 [as *L. labialis*], Fauth et al. 1989 [as *L. fragilis*], Heyer 1967, 1970b [both as *L. labialis*], 1978 [as *L. fragilis*], Hödl 1996 [as *L. labialis*], McDiarmid and Savage 2005 [as *L. labialis* (M)], Sasa and Solórzano 1995 [as *L. fragilis*], Savage 1973a,b

[both as *L. labialis*], 1980b [as *L. fragilis*], 2002 [as *L. labialis*], Savage and Villa 1986 [as *L. fragilis*], Scott et al. 1983 [as *L. fragilis*], Stafford 1998 [as *L. fragilis*], and Taylor 1952, 1954 [as *L. labialis*]); **El Salvador** (Heyer 1978 [as *L. fragilis*], Köhler et al. 2005 [as *L. fragilis*], Leenders and Watkins-Colwell 2004 [as *L. labialis*], Mertens 1952a,b [both as *L. labialis*], and Rand 1957 [as *L. labialis*]); **Guatemala** (Campbell 1998 [as *L. labialis*], Campbell and Vannini 1989 [as *L. fragilis*], Castañeda Moya et al. 2000 [as *L. labialis*], Crawford and Smith 2005 [as *L. labialis*], Duellman 1963 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Mendelson 1990 [as *L. fragilis*], Schmidt 1941 [as *L. labialis* (M)], and Stuart 1934, 1935, 1937, 1948, 1950, 1954, 1958, 1963 [all as *L. labialis*]); **Honduras** (Dunn and Emlen 1932 [as *L. labialis* and *L. melanotus* (sic) in part], Espinal et al. 2001 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Köhler 1999b [as *L. labialis*], Lynch and Fugler 1965 [as *L. labialis*], McCranie et al. 2002 [as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], McCranie and Wilson 2002 [as *L. labialis*],

- Meyer and Wilson 1971 [as *L. labialis* and *Scinax stauferi*, in part, {see McCranie and Wilson 2002, p. 325}], and Wilson et al. 1979, 1986 [both as *L. labialis*], 1991 [as *L. fragilis*]; **Mexico** (Anonymous 1998 [as *L. labialis*], Barbour 1914 [as *L. albilabris* (S)], Boulenger 1881 [as *L. albilabris* in part (M)(S)], 1882 [as *L. fragilis*], Brattstrom and Adis 1952 [as *L. labialis*], Brocchi 1877 [as *L. fragilis* and *L. caliginosus* in part], 1882 [as *L. fragilis*, *L. labialis* and *L. caliginosus* in part], Casas-Andreu et al. 1996 [as *L. labialis*], 2004 [as *L. fragilis*], Chrapliwy and Fugler 1955 [as *L. labialis*], Cope 1870 [as *Cystignathus gracilis*], 1879 [as *C. gracilis* and *C. labialis*], Davis and Dixon 1965 [as *L. labialis*], Davis and Smith 1953 [as *L. labialis*], Dixon and Heyer 1968 [as *L. labialis*], Duellman 1954, 1958a,b, 1960, 1961, 1965a,b [all as *L. labialis*], Dugès 1896 [as *L. labialis*], Dundee et al. 1986 [as *L. labialis*], Flores-Villela 1993a [as *L. labialis*], 1993b [as *L. cf. labialis-fragilis*], Flores-Villela et al. 1991 [as *L. labialis*], Gadow 1905, 1910 [both as *L. albilabris*], Gaige 1936 [as *L. labialis*], Goin 1959 [as *L. labialis*], Günther 1900 [as *L. albilabris*], 1902 [as *L. albilabris* in part], Hartweg and Oliver 1940 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Himmelstein 1981 [as *L. labialis*], Holman 1970, 2003 [both as *L. cf. L. labialis*], Ives 1892 [as *L. labialis*], Kellogg 1932 [as *L. albilabris*], Lazcano-Barrero et al. 1992 [as *L. fragilis*], Lee 1980, 1996, 2000 [all as *L. labialis*], Liner 1992a,b [both as *L. labialis*], Liner and Dundee 1969 [as *L. labialis*], Maldonado-Koerdell 1949, 1953 [both as *L. labialis*], Martin 1958 [as *L. labialis*], Martín del Campo 1953 [as *L. labialis*], Martínez Gracida 1891 [as *C. gracilis* and *C. labialis*], Maslin 1963a,b [both as *L. labialis*], Mata-López and León-Règagnon 2005 [as *L. labialis*], Müller 1884 [as *L. albilabris*], Pelcastre Villafuerte 1991 [as *L. labialis*], Pelcastre Villafuerte and Flores-Villela 1992 [as *L. labialis*], Pérez-Higareda et al. 1987 [as *L. fragilis*], Pineda and Haiffter 2004 [as *L. labialis*], Pineda et al. 2005 [as *L. fragilis*], Pozo de la Tijera et al. 1991 [as *L. labialis*], Pyburn 1963, 1967 [both as *L. labialis*], Ramírez Granados and Guzmán del Próo 1963 [as *L. labialis* (M)], Reddell 1977, 1981 [both as *L. labialis*], Reese and Firschein 1950 [as *L. labialis*], Rendón R. et al. 1998 [as *L. labialis*], Ruthven 1912 [as *L. albilabris*], Schmidt and Shannon 1947 [as *L. labialis*], Schmitter-Soto et al. 2002 [as *L. labialis* (M)], Shreve 1957 [as *L. mystaceus labialis*], Smith 1938, 1947 [both as *L. labialis*], Smith and Smith 1976b [as *L. labialis*], Smith and Taylor 1948, 1966 [both as *L. labialis*], Smith and Darling 1952 [as *L. labialis*], Smith and Smith 1952 [as *L. labialis*], Starrett 1968 [as *L. labialis*], Stejneger and Barbour 1933 [as *L. albilabris*], 1939, 1943 [both as *L. labialis*], Stuart 1958 [as *L. labialis* (M)], Sumichrast 1880 [as *C. gracilis*], 1881 [as *C. labialis*], 1882a,b [both as *C. gracilis* and *C. labialis*], Taylor 1949, 1953 [both as *L. labialis*], Taylor and Smith 1945 [as *L. labialis*], Torres-Orozco et al. 2002 [as *L. labialis*], Urbina-Cardona and Reynoso 2005 [as *L. fragilis*], and Werler and Smith 1952 [as *L. labialis*]; **Nicaragua** (Heyer 1978 [as *L. fragilis*], Köhler 1999a, 2001 [both as *L. labialis*], Köhler et al. 2005 [as *L. fragilis*], Noble 1918 [as *L. albilabris*], Schmitt 1994 [as *L. labialis*], Vences and Schmitt 1992 [as *L. labialis*], and Villa 1972 [as *L. labialis*]); **Panama** (Bernal and Ron 2004 [as *L. fragilis*], Busack 1966 [as *L. labialis*], Dunn 1931, 1933a,b [all as *L. labialis*], Fouquette 1960a,b [both as *L. labialis*], Heyer 1978 [as *L. fragilis*], Ibáñez D. et al. 1995, 1997 [both as *L. labialis*], Martínez Cortés 1984 [as *L. fragilis*], Nemuras 1968 [as *L. labialis*], Ponssa 2004 [as *L. labialis*], Rand and Myers 1990 [as *L. labialis*], Summers 2002 [as *L. labialis*], Swanson 1945 [as *L. labialis*], Taylor 1952 [as *L. labialis* (S)], Tejera Nuñez and Dupuy Loo 1994 [as *L. fragilis*], 2003 [as *L. labialis*], Young et al. 1999 [as *L. labialis*], and Zweifel 1964 [as *L. labialis*]); **United States** (Bartlett 1999 [as *L. labialis*], Bartlett and Bartlett 1999 [as *L. labialis*], Blair 1957, 1968 [both as *L. labialis*], Brown 1950 [as *L. labialis*], Conant 1958, 1975 [both as *L. labialis*], Conant and Collins 1991, 1998 [both as *L. labialis*], Dixon 1987 [as *L. fragilis*], 2000 [as *L. labialis*], Fouquette 1960b [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Livezey and Wright 1947 [as *L. labialis*], Mulaik 1937 [as *L. labialis*], Pratt 1935 [as *L. albilabris* (sic)], Raun and Gehlbach 1972 [as *L. labialis*], Schmidt 1953 [as *L. labialis*], Stejneger and Barbour 1933 [as *L. albilabris*], 1939, 1943 [both as *L. labialis*], Taylor 1932 [as *L. albilabris*], Travis et al. 1999 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], Wright 1935 [as *L. albilabris* in part], Wright and Wright 1938, 1949 [both as *L. labialis*], and Zim and Smith 1956 [as *L. labialis*]); **Venezuela** (Barrio-Amorós 1998 [as *L. labialis*], 2004 [as *L. fragilis*], Bisbal E. 1990 [as *L. fragilis*], Dixon and Staton 1976 [as *L. labialis*], Gorzula and Señaris 1999 [as *L. labialis*], Heyer 1978 [as *L. fragilis*], Hoogmoed and Gorzula 1979 [as *L. labialis*], La Marca 1992, 1995, 1997 [all as *L. labialis*], Mijares-Urrutia and Arends R. 2000 [as *L. labialis*], Öser 1934 [as *L. labialis*], Péfaur and Díaz de Pascual 1987 [as *L. fragilis*], Roca Perea 1982 [as *L. labialis*], and Staton and Dixon 1977 [as *L. labialis*]).
- **FOSSIL RECORD.** Hamblin (1984) noted a frog tibiofibula from Late Postclassic Cozumel Mayan excavations that could not be differentiated among *L. fragilis* (as *L. labialis*), *L. melanonotus*, or *Eleutherodactylus laticeps*. Holman (1970, as *L. cf. L. labialis*) tentatively assigned fossils of one left and two right ilia from the posterior parts of pelvic girdles (MU 8088) from the Pleistocene of Cueva de Abra, "... near the Pan American Highway, 10 kilometers north-northeast of the village of Antiguo Morelos, Tamaulipas, Mexico. ..." (p. 154) to this species. Carroll and Winer (1977, as *L. labialis*), Flores-Villela (1993a, as *L. cf. labialis-fragilis*), Holman (2003, as *L. cf. L. labialis*), and Sanchiz (1998, as *L. cf. labialis*) referred to the Tamaulipan fossils.
- **PERTINENT LITERATURE.** Heyer (1971 as *L. labialis*, 1978 as *L. fragilis*) published the most inclusive information on the species. The literature below is organized by topic. The symbol (M) after a citation stands for a mention of the species of interest only to a bibliophile and (S) indicates a secondary source:

bibliographic information and lists (Auth 1994 [as *L. labialis*], Beltz 1995 [as *L. fragilis*], Campbell 1999 [as *L. labialis*], Dixon 1993 [as *L. labialis*], Dixon and Liner 2003 [as *L. labialis*], La Marca 1992 [as *L. labialis*], Liner 1992c [as *L. labialis* in part], 1995, 1997, 1998, 1999 [all as *L. labialis*], Liner and Walley 1997 [as *L. labialis* in part], Péfaur 1992 [as *L. fragilis*], Savage 1980c [as *L. fragilis*], Savage and Villa 1986 [as *L. fragilis*], Smith and Smith 1973 [as *L. albilabris* and *L. labialis*], 1969, 1976b, 1993 [all as *L. labialis*], Taylor 1944 [as *L. albilabris*], 1947 [as *L. albilabris* and *L. labialis*], Travis et al. 1999 [as *L. labialis*], Villa 1983 [as *L. fragilis*], Villa et al. 1988 [as *L. fragilis*], and Walley 2000 [as *L. labialis*]); **biogeography** (Barrera 1963 [as *L. labialis*], Blair 1950 [as *L. labialis*], 1982 [as White-lipped Frog], Campbell 2001 [as *L. fragilis*], Cei 1962 [as *L. albilabris*], 1968 [as *L. labialis* (M)], Duellman 1954, 2001 [as *L. labialis*], Gadow 1930 [as *L. albilabris* (M)], Heyer 1978, 1988 [both as *L. fragilis*], Heyer and Maxson 1982 [as *L. fragilis* (M)], Johnson 1989, 1990 [both as *L. fragilis*], Lee 1980 [as *L. labialis*], Lynch and Suárez-Mayoraga 2004 [as *L. labialis*], Martin 1958 [as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], Mello Leitão 1947 [as *L. albilabris* (M)], Meyer and Meerman 2001 [as *L. labialis*], Müller 1973 [as *L. labialis*], Owen and Dixon 1989 [as *L. fragilis*], Péfaur and Rivero 2000 [as *L. labialis*], Ramírez-Bautista and Nieto Montes de Oca 1997 [as *L. labialis*], Rivero-Blanco and Dixon 1979 [as *L. fragilis*], Savage 2002 [as *L. labialis*], Smith and Buechner 1947 [as *L. labialis* (M)], Stuart 1950, 1954 [both as *L. labialis*], Wilson and McCranie 1998 [as *L. labialis*], and Wilson et al. 2001 [as *L. labialis*]); **book review** (Killebrew 1990 [as *L. fragilis*], and Lockington 1884 [as *L. fragilis*]); **call and call parameters** (Barrio 1965 [as *L. labialis* (S)], Bernal et al. 2004 [as *L. fragilis*], Bernal and Ron 2004 [as *L. fragilis*], Bevier 1995, 1997 [both as *L. labialis*], Blair 1963 [as *L. labialis* (M)], Campbell 1998 [as *L. labialis*], Dixon and Heyer 1968 [as *L. labialis*], Duellman 1960, 1967 [both as *L. labialis*], Duellman and Trueb 1966 [as *L. labialis*], Dunn 1933a,b [as *L. labialis*], Eggermont 1988 [as *L. labialis* (S)], Heyer 1978 [as *L. fragilis*], Kime et al. 2000 [as *L. fragilis*], Martin 1958 [as *L. labialis*], Mulaik 1937 [as *L. labialis*], Neill and Allan 1961 [as *L. labialis*], Öser 1934 [as *L. labialis*], Roca Perea 1982 [as *L. labialis*], Rose et al. 1988 [as *L. labialis*], Ryan 1985 [as *L. labialis*], Salthe and Mecham 1974 [as *L. labialis*], Savage 2002 [as *L. labialis*], Schmidt and Shannon 1947 [as *L. labialis*], Staton and Dixon 1977 [as *L. labialis*], Stuart 1948 [as *L. labialis*], Wells 2001 [as *L. labialis* (S)], Wilczynski et al. 2002 [as *L. labialis* (sic)], Wright and Wright 1933 [as *L. albilabris* in part (S)], 1942 [as *L. labialis* (S)], and Wright and Wright 1949 [as *L. labialis* (S)]; **captive breeding and care** (Klingelhöffer and Scherpner 1956 [as *L. labialis*], Öser 1934 [as *L. labialis*], and Sennft 1935 [as *L. labialis*]); **checklists** (Auth 1994 [as *L. labialis*], Brown 1950 [as *L. labialis*], Díaz de León 1904 [as *L. albilabris* and *L. fragilis*], Dowling 1975 [as *L. labialis*], Gorham 1974 [as *L. labialis*], Henderson and Hoevers 1975 [as *L. labialis*], Köhler 1999a [as *L. labialis*], Leenders 2001 [as *L. labialis*], McDiarmid 1987

[as *L. fragilis*], Meerman 1993 [as *L. labialis*], Meyer and Wilson 1971 [as *L. labialis*], Mijares-Urrutia and Arends R. 2000 [as *L. labialis*], Neill 1965 [as *L. labialis*], Péfaur 1992 [as *L. fragilis*], Péfaur and Rivero 2000 [as *L. labialis*], Pérez-Ramos et al. 2000 [as *L. labialis*], Pratt 1935 [as *L. alibilebris* (sic)], Schmidt 1953 [as *L. labialis*], Scott et al. 1983 [as *L. fragilis*], Señaris and MacCulloch 2005 [as *L. labialis*], Smith and Taylor 1948, 1966 [both as *L. labialis*], Stafford 1998 [as *L. fragilis*], Stejneger and Barbour 1933 [as *L. albilabris* in part], 1939, 1943 [both as *L. labialis*], Stuart 1963 [as *L. labialis*], Thomas 1974, 1976 [both as *L. labialis*], Villa 1971 [as *L. labialis*], 1983 [as *L. fragilis*], and Wilson 1983 [as *L. fragilis*]); **conservation** (Anonymous 1998 [as *L. labialis*], Ashton 1976 [as *L. labialis*], Bartlett and Bartlett 1999 [as *L. labialis*], Casas-Andreu et al. 1996 [as *L. labialis*], 2004 [as *L. fragilis*], Chaney 1982 [as *L. fragilis*], Coastal Impact Monitoring Program 1995 [as *L. fragilis*], Dixon 1987 [as *L. fragilis*], 2000 [as *L. labialis*], Donnelly and Crump 1998 [as *L. labialis*], Edwards et al. 1989 [as *L. fragilis*], Flores-Villuela (sic) 1980 [as *L. labialis*], García 2006, Garrett and Barker 1987 [as *L. fragilis*], González et al. 1999 [as *L. labialis*], Greenbaum and Komar 2005 [as *L. fragilis*], Heyer 2005 [as *L. fragilis*], Jiménez-Cruz et al. 1998 [as *L. labialis*], Köhler 2001 [as *L. labialis*], Lazcano-Barrero et al. 1992 [as *L. fragilis*], Levell 1995, 1997 [both as *L. labialis*], Lips et al. 2003 [as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], Meyer and Meerman 2001 [as *L. labialis*], Péfaur and Rivero 2000 [as *L. labialis*], Pineda and Halffter 2004 [as *L. labialis*], Pozo de la Tijera et al. 1991 [as *L. labialis*], Sánchez et al. 1999 [as *L. labialis*], Tejera Nuñez and Dupuy Loo 2003 [as *L. labialis*], Wilson and McCranie 2003 [as *L. labialis*], and Young et al. 1999 [as *L. labialis*], 2004 [as *L. fragilis*]); **development** (Mulaik 1937 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part (S)], 1942 [as *L. labialis* (S)], and Wright and Wright 1949 [as *L. labialis* (S)]; **distribution** (Duellman and Sweet 1999 [as *L. labialis*], Iremonger et al. 1994 [as *L. fragilis*], Leenders 2003 [as *L. labialis* (M)], Limeses 1969 [as *L. labialis* (M)], and Wilson and Hahn 1973 [as *L. labialis*]); **ecology, natural history, reproduction** (Albert et al. 2005 [as *L. labialis*], Bernal and Ron 2004 [as *L. fragilis*], Blair 1976 [as *L. labialis*], Bogert 1969 [as *L. labialis* (M)(S)], Brattstrom and Adis 1952 [as *L. labialis*], Brazil and Vellard 1925 [as *L. fragilis* = *L. ?*], Campbell 1998 [as *L. labialis*], Campbell and Lamar 2004 [as *L. fragilis*], Conant 1955 [as *L. labialis*], Cuentas Montalvo et al. 2002 [as *L. labialis*], Davis 1951 [as *L. labialis*], Dixon and Heyer 1968 [as *L. labialis*], Duellman 1960, 1961, 1965b, 1966 [all as *L. labialis*], 1990 [as *L. fragilis*], Echternacht 1977 [as *L. labialis*], Espinal et al. 2001 [as *L. labialis*], Fauth et al. 1989 [as *L. fragilis*], Gadow 1901 [as *L. albilabris* in part (M)], Gorzula and Señaris 1999 [as *L. labialis*], Griffiths 1963 [as *L. labialis* (M)(S)], Heyer 1967, 1970b [both as *L. labialis*], Himmelstein 1981 [as *L. labialis*], Höbel 2004a,b [both as *L. labialis*], Ibáñez D. et al. 1997, 1999a [both as *L. labialis*], Ives 1892 [as *L. labialis*], Jameson 1955 [as *L. labialis*], Klingelhöffer and Scherpner 1956 [as *L. labialis*], La

- Marca and Garcia P. 1987 [as *L. fragilis*], Lescure 1972 [as *L. labialis* (**M**)(**S**)], Livezey and Wright 1947 [as *L. labialis*], Maslin 1963a [as *L. labialis*], McCoy and Censky 1992 [as *L. fragilis*], McCranie et al. 2006 [as *L. fragilis*], McDiarmid and Foster 1981 [as *L. fragilis*], Mulaik 1937 [as *L. labialis*], Neill and Allan 1961 [as *L. labialis*], Oliver 1955 [as *L. labialis*], Öser 1933 [as *L. labialis*], Péfaur and Díaz de Pascual 1987 [as *L. fragilis*], Philipbosian et al. 1974 [as *L. labialis* (**S**)], Pineda and Halffter 2004 [as *L. labialis*], Pineda et al. 2005 [as *L. fragilis*], Pocai 1941 [as *L. fragilis* = *L. ?* (**S**)], Ponssa 2004 [as *L. labialis*], Pyburn 1963 [as *L. labialis*], Ramirez et al. 1998 [as *L. labialis* (**M**)], Rand and Myers 1990 [as *L. labialis*], Reese and Firschein 1950 [as *L. labialis*], Roca Perea 1982 [as *L. labialis*], 1985 [as *L. fragilis*], Rossman 1963 [as *L. labialis*], Ruthven 1912 [as *L. albilabris*], Salthé and Mecham 1974 [as *L. labialis* (**S**)], Sasa and Solórzano 1995 [as *L. fragilis*], Savage 2002 [as *L. labialis*], Sazima 1975 [as *L. labialis* (**S**)], Schmitt 1994 [as *L. labialis*], Scott and Limerick 1983 [as *L. fragilis*], Seib 1984 [as *L. labialis*], Solano 1987 [as *L. fragilis* (**S**)], Solórzano 2004 [as *L. labialis*], Stuart 1935, 1950, 1954 [all as *L. labialis*], Torres-Orozco et al. 2002 [as *L. labialis* (**S**)], Urbina-Cardona and Reynoso 2005 [as *L. fragilis*], Vences and Schmitt 1992 [as *L. labialis*], Villa 1969a,b, 1970 [all as *L. labialis*], Vogt 1997 [as *L. labialis*], Wilczynski et al. 2002 [as *L. labialis* (sic)], Wright and Wright 1933 [as *L. albilabris* in part (**S**)], 1942 [as *L. labialis* (**S**)], Wright and Wright 1938, 1949 [both as *L. labialis* (**S**)], and Zweifel 1964 [as *L. labialis*]; **evolution** (Blair 1976 [as *L. labialis*], Heyer 1969a [as *L. labialis*], 1978 [as *L. fragilis*], and Roca Perea 1982 [as *L. labialis*]); **faunal accounts** (La Marca 1992 [as *L. labialis*], Meyer and Foster 1996 [as *L. labialis*], and Sasa Marin 2000); **faunal lists** (Aranda and Guzmán 1999, Cope 1887 [as *L. gracilis* in part and *L. labialis*], Dugès 1896 [as *L. labialis*], Köhler 1999b [as *L. labialis*], and Pearse 1977 [as *L. labialis*]); **field guides** (Bartlett and Bartlett 1999 [as *L. labialis*], Behler and King 1979 [as *L. labialis*], Beletsky 1999 [as *L. labialis*], Cochran and Goin 1970 [as *L. labialis*], Conant 1958, 1975 [both as *L. labialis*], Conant and Collins 1991, 1998 [both as *L. labialis*], Cuentas Montalvo et al. 2002 [as *L. labialis*], Garrett and Barker 1987 [as *L. fragilis*], Lee 2000 [as *L. labialis*], Meyer and Foster 1996 [as *L. labialis*], Renjifo and Lundberg 1999 [as *L. fragilis*], Smith 1978 [as *L. labialis*], and Wainwright 2000 [as *L. fragilis*]); **habitat** (Augustine et al. 1998 [as *L. labialis*], Campbell 2001 [as *L. fragilis*], Cuentas Montalvo et al. 2002 [as *L. labialis*], Dixon and Heyer 1968 [as *L. labialis*], Duellman 1960, 1965b [both as *L. labialis*], 1990 [as *L. fragilis*], Espinal et al. 2001 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*], Galindo-Leal et al. 2003 [as *L. labialis*], Goin et al. 1978 [as *L. labialis* (**S**)], Hartweg and Oliver 1940 [as *L. labialis*], Himmelstein 1981 [as *L. labialis*], Hödl 1996 [as *L. labialis*], Ibáñez D. et al. 1995, 1997 [both as *L. labialis*], Kellogg 1932 [as *L. albilabris* (**S**)], Lazcano-Barrero et al. 1992 [as *L. fragilis*], Lee 1996, 2000 [both as *L. labialis*], Leenders and Watkins-Colwell 2004 [as *L. labialis*], Martin 1958 [as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], Mendelson 1990 [as *L. fragilis*], Neill 1965 [as *L. labialis*], Neill and Allan 1961 [as *L. labialis*], Nemuras 1968 [as *L. labialis*], Pineda and Halffter 2004 [as *L. labialis*], Pineda et al. 2005 [as *L. fragilis*], Rand 1957 [as *L. labialis*], Reddell 1981 [as *L. labialis*], Rendón R. et al. 1998 [as *L. labialis*], Roca Perea 1982 [as *L. labialis*], Savage 2002 [as *L. labialis*], Schmidt and Shannon 1947 [as *L. labialis*], Schmitter-Soto et al. 2002 [as *L. labialis* (**M**)], Stafford 1998 [as *L. fragilis*], Stuart 1935, 1948 [both as *L. labialis*], Taylor 1932 [as *L. albilabris*], 1954 [as *L. labialis*], Tejera Nuñez and Dupuy Loo 2003 [as *L. labialis*], Urbina-Cardona and Reynoso 2005 [as *L. fragilis*], Vences and Schmitt 1992 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part (**S**)], 1942 [as *L. labialis*], and Wright and Wright 1938, 1949 [both as *L. labialis* (**S**)]; **handbooks** (Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], and Wright and Wright 1949 [as *L. labialis*]); **historical papers** (McDiarmid 1995 [as *L. labialis* (**M**)]; **inventories** (Bisbal 1990 [as *L. fragilis*], Ibáñez D. et al. 1995, 1997 [both as *L. labialis*], and Urbina-Cardona and Reynoso 2005 [as *L. fragilis*]); **karyotypes** (Bogart 1974 [as *L. labialis*], Gilboa 1975 [as *L. labialis* (**S**)], Heyer 1978 [as *L. fragilis* (**S**)], King 1990 [as *L. labialis* (**S**)], Kuramoto 1990 [as *L. fragilis* (**S**)], León 1970 [as *L. labialis*], Morescalchi 1979 [as *L. labialis*], Rada de Martínez 1976 [as *L. labialis*], and Savage 2002 [as *L. labialis* (**S**)]; **keys** (Altig 1970 [as *L. labialis*], 1987 [as *L. fragilis*], Ballinger and Lynch 1983 [as *L. fragilis*], Boulenger 1882 [as *L. fragilis*], Campbell 1998 [as *L. labialis*], Chaney 1982 [as *L. fragilis*], Cope 1879 [as *L. gracilis* and *L. labialis*], Cuentas Montalvo et al. 2002 [as *L. labialis*], Dixon 1987 [as *L. fragilis*], 2000 [as *L. labialis*], Dunn 1931 [as *L. labialis*], Flores-Villela et al. 1987 [as *L. fragilis*], Henderson and Hoevers 1975 [as *L. labialis*], Heyer 1970b [as *L. labialis*], 1978 [as *L. fragilis*], Köhler 1999a, 2001 [both as *L. labialis*], Köhler et al. 2005 [as *L. fragilis*], Lee 1996 [as *L. labialis*], Lips and Savage 1996 [as *L. labialis*], Livezey and Wright 1947 [as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], Mertens 1952a [as *L. labialis*], Meyer and Wilson 1971 [as *L. labialis*], Nemuras 1968 [as *L. labialis*], Nieden 1923 [as *L. fragilis*], Orton 1952 [as *L. labialis*], Powell et al. 1998 [as *L. labialis*], Savage 1980a, 1980c, 2002 [all as *L. labialis*], Savage and Villa 1986 [as *L. fragilis*], Smith 1978 [as *L. labialis*], Smith and Taylor 1948, 1966 [both as *L. labialis*], Stuart 1963 [as *L. labialis*], Sumichrast 1882b [as *L. gracilis* and *L. labialis* (**S**)], Villa 1972 [as *L. labialis*], Wilson and McCranie 1993 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], and Wright and Wright 1938, 1949 [both as *L. labialis*]; **lists of specimens in collections** (Auth et al. 2000 [as *L. labialis*], Flores-Villela et al. 1991 [as *L. labialis*], Müller 1884 [as *L. albilabris*], Tejera Nuñez and Dupuy Loo 1994 [as *L. fragilis*], and 2003 [as *L. labialis*]; **morphology** (Altig and Johnston 1986 [as *L. labialis*], Bevier 1995 [as *L. labialis*], Cardozo 2004 [as *L. labialis* (**S**)], Duellman 1961 [as *L. labialis*], Gaige 1936 [as *L. labialis*], Gans and Pyles 1983 [as *L. labialis*], Goin 1959 [as *L. labialis*], Haas 1996 [as

L. fragilis (S)); Hailman 1976 [as *L. labialis*], Helling 1938 [as *L. labialis*], Larson and de Sá 1998 [as *L. labialis*], Lee 1993 [as *L. labialis*], Martin 1972 [as *L. labialis*], Neill 1965 [as *L. labialis*], Neill and Allan 1961 [as *L. labialis*], Nussbaum 1982 [as *L. labialis*], Ponssa 2001 [as *L. labialis*], Roca Perea 1982 [as *L. labialis*], Starrett 1968 [as *L. labialis*], Villa 1972 [as *L. labialis*], Wever 1985 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part (S)], 1942 [as *L. labialis* (S)], and Wright and Wright 1949 [as *L. labialis* (S)]; **nomenclature and taxonomy** (Bogert and Oliver 1945 [as *L. fragilis*], Crother et al. 2000 [as *L. labialis*], Dubois and Heyer 1992 [as *L. labialis*], Flores-Villela and Canseco-Márquez 2004 [as *L. fragilis*], Heyer 1971, 1974 [both as *L. labialis*], 2002 [as *L. fragilis*], Kellogg 1932 [as *L. albilabris*], Savage 2002 [as *L. labialis*], Schmidt 1928 [as *L. labialis* (M)], Smith 1987 [as *L. fragilis*], Smith and Smith 1976b [as *L. labialis*], and Taylor 1932 [as *L. albilabris*]); **non-technical literature** (Albert et al. 2005 [as *L. labialis*], Ballinger and Lynch 1983 [as *L. fragilis*], Bartlett 1999 [as *L. labialis*], Beletsky 1999 [as *L. labialis*], Bernal 2002 [as *L. fragilis*], Blair 1957, 1968 [both as *L. labialis*], Bruno 1969 [as *L. labialis*], Conant 1997 [as *L. labialis* (M)], Duellman 2003 [as *L. labialis*], Echternacht 1977 [as *L. labialis*], Flores-Villela and Hernández Gómez 1988 [as *L. labialis*], Frazer 1967a,b [both as *L. labialis*], Freiberg 1972 [as *L. labialis*], Freytag 1967 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*], Krywicki 2001 [as *L. labialis*], Leviton 1971 [as *L. labialis*], Mohr 1963 [as *L. labialis*], Norman 1998 [as *L. fragilis*], Obst et al. 1984, 1988 [both as *L. labialis*], Smyth 1962 [as *L. labialis*], and Zim and Smith 1956 [as *L. labialis*]); **parasitology** (Earl 1974 [as *L. labialis*], Mata-López and León-Régagnon 2005 [as *L. labialis*], and Metcalf 1923 [as *L. albilabris* in part and *L. gracilis*]); **physiology** (Bevier 1995, 1997 [both as *L. labialis*], Brazil and Vellard 1926 [as *L. fragilis*], Hailman and Jaeger 1974 [as *L. labialis*], Jaeger and Hailman 1973 [as *L. labialis*], and Wells 2001 [as *L. labialis* (S)]); **relationships and systematics** (Barbour 1930, 1935 [both as *L. labialis* (M)], Barrio 1973 [as *L. labialis* (M)], Bogart 1974 [as *L. labialis*], Crawford and Smith 2005 [as *L. labialis*], Crother 1999 [as *L. labialis* (M)], Heyer 1978 [as *L. fragilis*], Heyer et al. 2005 [as *L. labialis*], Heyer and Diment 1974 [as *L. labialis*], Kluge and Farris 1969 [as *L. labialis*], Larson and de Sá 1998 [as *L. labialis*], Lynch 1971 [as *L. labialis*], Maxson and Heyer 1988 [as *L. fragilis*], Miyamoto 1981 [as *L. fragilis*], and Starrett 1968 [as *L. labialis*]); **species accounts** (Boulenger 1882 [as *L. fragilis*], Campbell 1998 [as *L. labialis*], Heyer 1970b, 1971 [both as *L. labialis*], 1978 [as *L. fragilis*], Ibáñez D. et al. 1999a [as *L. labialis*], Köhler et al. 2005 [as *L. fragilis*], Lee 1996, 2000 [both as *L. labialis*], McCranie et al. 2006 [as *L. fragilis*], McCranie and Wilson 2002 [as *L. labialis*], Meyer and Wilson 1971 [as *L. labialis*], Nieden 1923 [as *L. fragilis*], Savage 2002 [as *L. labialis*], Taylor 1954 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], and Wright and Wright 1949 [as *L. labialis*]); **species comparisons** (Barbour 1906 [as *L. fragilis* (M)], 1917, 1937 [both as *L.*

labialis (M)], Brocchi 1877 [as *C. fragilis*], Cascon and Peixoto 1985 [as *L. fragilis*], Cope 1894 [as *L. labialis*], Dunn 1940 [as *L. labialis*], Gaige 1936 [as *L. labialis*], Gallardo 1964 [as *L. labialis*], Heyer 1969b, 1970a,b, 1995 [all as *L. labialis*], 1978, 1983 [both as *L. fragilis*], Heyer et al. 2002 [as *L. fragilis*], Heyer and Heyer 2001 [as *L. labialis*], 2002 [as *L. fragilis*], Heyer and Juncá 2003 [as *L. fragilis*], Heyer and Thompson 2000 [as *L. labialis*], Larson and de Sá 1998 [as *L. labialis*], Orton 1951, 1952 [both as *L. labialis*], Savage 2002 [as *L. labialis*], Stejneger 1904 [as *L. albilabris*], Villa 1972 [as *L. labialis*], Weimer et al. 1993 [as *L. fragilis*], and Wettstein 1934 [as *L. albilabris*]); **specimens or taxonomic lists** (Acosta-Galvis 2000 [as *L. labialis*], Ananjeva et al. 1988 [as *L. fragilis*], Cochran 1961 [as *L. labialis*], Duellman 1993, 2003 [both as *L. labialis*], Dueñas et al. 2001 [as *L. labialis*], Flores-Villela 1993a [as *L. labialis*], Frost 1985 [as *L. fragilis*], Glaw et al. 2000 [as *L. labialis*], Gorham 1966 [as *L. labialis*], Guibé 1950 [as *L. fragilis*], Harding 1983 [as *L. fragilis*], Ibáñez D. et al. 2001 [as *L. labialis*], Köhler 2001 [as *L. labialis*], La Marca 1995, 1997 [both as *L. labialis*], Lazcano et al. 2006, Mertens 1952b [as *L. labialis*], Páez et al. 2002 [as *L. labialis*], Ruiz-Carranza et al. 1996 [as *L. fragilis*], Smith and Smith 1976b [as *L. labialis*], Vogt et al. 1997 [as *L. labialis*], and Wilson and McCranie 1994 [as *L. labialis*]).

• **NOMENCLATURE HISTORY.** Both Brocchi (1877) and Cope (1877) penned species descriptions that were used by the scientific community for *L. fragilis* for various time periods. Dubois and Heyer (1992) demonstrated that *Cystignathus fragilis* Brocchi 1877 had publication date priority over *Cystignathus labialis* Cope 1877. During the early years of publications dealing with *L. fragilis*, some authors thought that the frogs from Mexico and Middle America belonged to the same species as *Leptodactylus gracilis*, a South American species. Up until the seminal work of Boulenger (1882), *L. fragilis* was variously cited as *L. fragilis*, *L. gracilis*, or *L. labialis* (or as a species of the genus *Cystignathus*, a synonym of the genus *Leptodactylus*). Boulenger recognized two species that involved what is currently understood as *L. fragilis*: *L. fragilis* (1882:241) and *L. albilabris* (1882:245). Boulenger thought that the supposedly Mexican species described by Cope (*C. labialis*) represented the same species described from St. Thomas in the West Indies as *Cystignathus albilabris* Günther. Stejneger (1904) concurred with Boulenger's synonymy and commented at some length on the zoogeographical implausibility of the same species occurring in Puerto Rico and Mexico, concluding on page 562: "In suggesting accidental introduction by man I am fully aware that this explanation does not at first appear plausible, as there does not seem to be or to have been any direct route of communication between southern Mexico or Yucatan and Porto Rico or the Virgin Islands, but I offer it as the only possibility I can think of. The wrecking of a vessel with a cargo of logwood or mahogany a hundred years or more ago might account for this remarkable distribution." Barbour (1914:252–253) did not accept this explanation

in his treatment of the zoogeography of the herpetofauna of the West Indies but thought the two species were similar because: "It is more probable that the Porto Rican and mainland individuals have by some fortuitous parallelism become indistinguishable if they originally belonged to different stocks ... (p. 253)." Schmidt (1928) in his treatment of the herpetofauna of Puerto Rico and the Virgin Islands strongly disagreed that *L. labialis* was conspecific with *L. albilabris* and described diagnostic characters that differentiated the two from one another. Dunn (e.g. 1931) treated the Middle American frogs as *L. labialis*. Kellogg (1932:84–87) recounted the taxonomic history of the species and, based on examination of specimens at his disposal, disagreed with Schmidt and concurred with Boulenger and Stejneger and recognized the Mexican frogs as *L. albilabris*. Taylor (1932) used *L. albilabris* in his paper reporting the species for the first time in the United States. Gaige (1936:291) examined preserved specimens, agreed with Dunn's assessment, and identified the frogs from the Yucatan of Mexico as *L. labialis*. Mulaik (1937) was the first to use *L. labialis* for the species in the United States, again based on examination of specimens from the USA and the West Indies. Thus, from the early through the late 1930's, the northern (USA and Mexico) frogs were mostly reported as *L. albilabris* and the southern frogs (Guatemala through Panama) as *L. labialis*. From the late 1930's until 1978, the species was reported as *L. labialis*. Heyer (1978:31–32) reported that the juvenile type specimens of *Cystignathus labialis* were conspecific with the South American species *Leptodactylus mystacinus*. Cope (1877) reported on specimens from Mexico, Costa Rica, Panama, and Argentina. The locality given by Cope (1877:90) for *C. labialis* was: "The precise habitat of this species is at present uncertain. It is probably a part of Sumichrast's Mexican collection." Heyer (1978) placed *Cystignathus labialis* into the synonymy of *Leptodactylus mystacinus* (Burmeister 1861) and recognized *Leptodactylus fragilis* as the appropriate name for the species that occurs from Texas to Venezuela. The saga should have ended here but took an unfortunate twist (to the embarrassment of one of the authors of this account). Dubois and Heyer (1992) ignored Heyer's (1978) action placing *C. labialis* in the synonymy of *L. mystacinus* and placed *C. fragilis* Brocchi 1877 in the synonymy of *L. labialis* (Cope 1877) based on when the respective papers were published. Throughout the 1980s until 2002, *Leptodactylus labialis* was the name used for the species involved. Heyer (2002), after re-reading Heyer (1978) and re-examining Cope's type specimens, pointed out the error in Dubois and Heyer (1992) and resurrected *Leptodactylus fragilis* (Brocchi 1877) as the appropriate name for the species.

• **REMARKS.** The following common names have been used for *Leptodactylus fragilis*: **Acacueyatl** (Martínez Gracida 1891 [as *L. gracilis* and *L. labialis*]); **American White-lipped Frog** (DuBois and Heyer 1992 [as *L. labialis*], Young et al. 2004 [as *L. fragilis*]); **Cope's White-lipped Frog** (Frank and Ramus

1995 [as *L. labialis*]); **Mexican White-lipped Frog** (Blair 1957, 1968 [both as *L. labialis*], Cochran and Goin 1970 [as *L. labialis*], Conant 1958 [as *L. labialis*], Conant et al. 1956 [as *L. labialis*], Crother et al. 2000 [as *L. labialis*], 2003 [as *L. fragilis*], Dowling 1975 [as *L. labialis*], Holman 2003 [as *L. cf. L. labialis*], Leviton 1971 [as *L. labialis*], McDiarmid 1987 [as *L. fragilis*], Obst et al. 1988 [as *L. labialis*], Oliver 1955 [as *L. labialis*], Raun and Gehlbach 1972 [as *L. labialis*], Schmidt 1953 [as *L. labialis*], Thomas 1974, 1976 [both as *L. labialis*]); **Pfeiffrosch** (Sennft 1935 [as *L. labialis*]); **Rana** (Martínez Gracida 1891 [as *L. gracilis* and *L. labialis*]); **Rana de Labios Blancos** (Flores-Villela and Hernández Gómez 1988 [as *L. labialis*]); **Rana de Dedos Delgados de Labios Blancos** (proposed common Spanish name at www.learning.richmond.edu/Leptodactylus [as *L. fragilis*]); **Ranilla** (Martínez Gracida 1891 [as *L. gracilis* and *L. labialis*]); **Ranita** (Lee 1996 [as *L. labialis*]); **Ranitade Charco** (Beletsky 1999 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*], Liner 1994 [as *L. labialis*], Villa 1971 [as *L. labialis*], 1983 [as *L. fragilis*]); **Ranita de Charco Labio Blanco** (Köhler 2001 [as *L. labialis*]); **Ranita de Espumera de Labioblanco** (Campbell 1998 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*]); **Ranita de Labios Blancos** (Freiberg 1972 [as *L. labialis*]); **Ranita de la Hojarasca** (Beletsky 1999 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*], Lee 1996 [as *L. labialis*], Pozo de la Tijera et al. 1991 [as *L. labialis*]); **Ranita del Sabinal** (Galindo-Leal 2003 [as *L. labialis*]); **Rana Silbadora Labiblanca** (Norman 1998 [as *L. fragilis*], Wainwright 2000 [as *L. fragilis*]); **Sapo-Rana Sabiado** (Barrio-Amorós 1998 [as *L. labialis*]); **White-jawed Frog** (Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], Wright and Wright 1949 [as *L. labialis*]); **White-jawed Robber Frog** (Wright and Wright 1942 [as *L. labialis*], Wright and Wright 1938, 1949 [both as *L. labialis*]); **White-lipped Foam Frog** (Bernal and Ron 2004 [as *L. fragilis*], Campbell 1998 [as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*]); **White-lipped Frog** (Albert et al. 2005 [as *L. labialis*], Ashton 1976 [as *L. labialis*], Ballinger and Lynch 1983 [as *L. fragilis*], Bartlett 1999 [as *L. labialis*], Bartlett and Bartlett 1999 [as *L. labialis*], Behler and King 1979 [as *L. labialis*], Beletsky 1999 [as *L. labialis*], Blair 1982, Brown 1950 [as *L. labialis*], Chaney 1982 [as *L. fragilis*], Collins 1990, 1997 [both as *L. labialis*], Collins and Taggart 2002 [as *L. labialis*], Collins et al. 1978 [as *L. labialis*], 1979, 1982 [both as *L. fragilis*], Conant 1975, 1991, 1997 [all as *L. labialis*], Conant and Collins 1991, 1998 [both as *L. labialis*], Dixon 1987 [as *L. fragilis*], 1993, 2000 [both as *L. labialis*], Galindo-Leal 2003 [as *L. labialis*], Garrett and Barker 1987 [as *L. fragilis*], Krywicki 2001 [as *L. labialis*], Lee 1996, 2000 [both as *L. labialis*], Levell 1995, 1997 [both as *L. labialis*], Liner 1992b, 1994 [both as *L. labialis*], Meyer and Foster 1996 [as *L. labialis*], Stafford 1998 [as *L. fragilis*], Travis et al. 1999 [as *L. labialis*], Wright and Wright 1933 [as *L. albilabris* in part], 1942 [as *L. labialis*], Wright and Wright 1949 [as *L. labialis*], Zim and Smith 1956 [as *L. labialis*]); **White-lipped Thin-toed Frog** (proposed common English name at www.

learning.richmond.edu/*Leptodactylus* [as *L. fragilis*]; **White-lipped Toad** (Smith 1978 [as *L. labialis*]); **White-lipped Whistling Frog** (Norman 1998 [as *L. fragilis*], Wainwright 2000 [as *L. fragilis*]).

Volumes 3, 5, and 6 of Hobart and Rozella Smith's 'Synopsis of the Herpetofauna of Mexico' (1976a, 1977, and 1979) are included in this account because citations within them are referenced in later publications by these authors.

McCranie and Wilson (2002:444) do not state that tadpole tooth row P-1 is divided in *L. fragilis*. Their description is based on USNM 514731 (2 specimens in lot). Both specimens have the formula 2(2)/3(1), with the divided P-1 rows narrowly separated from each other. We suspect that other published citations of the formula 2(2)/3 (see Langone and de Sá 2005) also have narrowly separated P-1 rows and thus should be 2(2)/3(1).

The advertisement call description is based on published accounts by Bernal et al. (2004, as *L. fragilis* from Colombia); Fouquette (1960b, as *L. labialis* from Texas and Panama); Lee (1996, as *L. labialis* from Belize); Straughan and Heyer (1976, as *L. labialis* from Costa Rica) and analyses of calls from a Texas Memorial Museum recording (Tape Station 29) from Texas, Hidalgo County, 2 miles E Madero; the CD produced by Ibáñez D. et al. (1999b, as *L. labialis* from Panama); and USNM recording 225 cut 2 from Venezuela. The published information on advertisement calls did not contain information on all aspects of the call described in this account. Most available recordings lack information on air temperature at time of recording and size of the recorded male, thus the available information can not distinguish whether the observed variation in call parameters correlates with temperature, size of calling males, or populational variation.

• **ETYMOLOGY.** The name *fragilis*, meaning brittle, is derived from the Latin "frag", the root of "frango" (to break). It is unclear why the author used *fragilis* when naming this species.

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